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Shell variation in Australian *Notopala* (Gastropoda: Prosobranchia: Viviparidae)

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ABSTRACT

The viviparid snail *Notopala* is distributed throughout the rivers and other waterbodies of the northern tropical regions of Australia, extending south into the Lake Eyre and Murray-Darling Basins. Despite a recent examination of the Western Australian viviparids the taxonomy of a number of species, especially those from the Lake Eyre and Murray-Darling Basins, is unclear. Principal Components Analysis was used on seven shell measurements to determine which morphometric characters best delineate the species. Umbilicus width and aperture lip length explained most of the variation. The results suggest that there are four species of *Notopala* in Australia: *N. waterhousii* and *N. essingtonensis* in the north and north-west, *N. sublineata* in the Lake Eyre and Murray-Darling Basins and *N. hanleyi* in the Murray-Darling Basin. With the apparent extinction of both species of *Notopala* in the natural environment of the Murray-Darling Basin, the population of *N. hanleyi* surviving in a Murray irrigation pipeline and the population of *N. sublineata* in the Lake Eyre Basin have significant conservation value.

INTRODUCTION

The Viviparidae is a family of medium to large prosobranch snails that commonly occur in freshwater lotic and lentic systems throughout the world (Browne, 1978). They are viviparous, as their name suggests. The family in Australia is represented by *Notopala, Centropala,* and *Larina* (Smith, 1992). *Notopala* Cotton, 1935 contains at least four species in the north of the continent, extending south-east into the Lake Eyre and Murray-Darling Basins (McMichael, 1967). *Centropala* Cotton, 1935 is represented by *C. lirata* (Tate, 1887), found only in the Lake Eyre Basin (Smith, 1992). The sole species of *Larina, L. strangei* A. Adams, 1854, is restricted to coastal north-east Queensland (Smith, 1992).

Cotton (1935a) erected the genus *Notopala*, with *Notopala hanleyi* Frauenfeld, 1864 as the type, for those Australian viviparids exhibiting a distinctive fine spiral microsculpture of the shell. Sculpturing, however, is not restricted to Australian taxa, which have many anatomic and morphological similarities to certain south-east Asian genera (Stoddart, 1982). This suggests a need for a generic revision of the Australian viviparids.

The taxonomy of *Notopala* is confounded by several ill-justified synonymies (cf. Iredale, 1943; Smith, 1978; Smith & Kershaw, 1979). The diagnostic criteria are essentially morphometric (cf. Cotton, 1935b, Stoddart, 1982), and there is a need for a more detailed assessment based on both morphological and molecular characters. This paper attempts to clarify the status of *Notopala* in central and southern Australia by using multivariate analysis of morphological data to better delineate taxa.

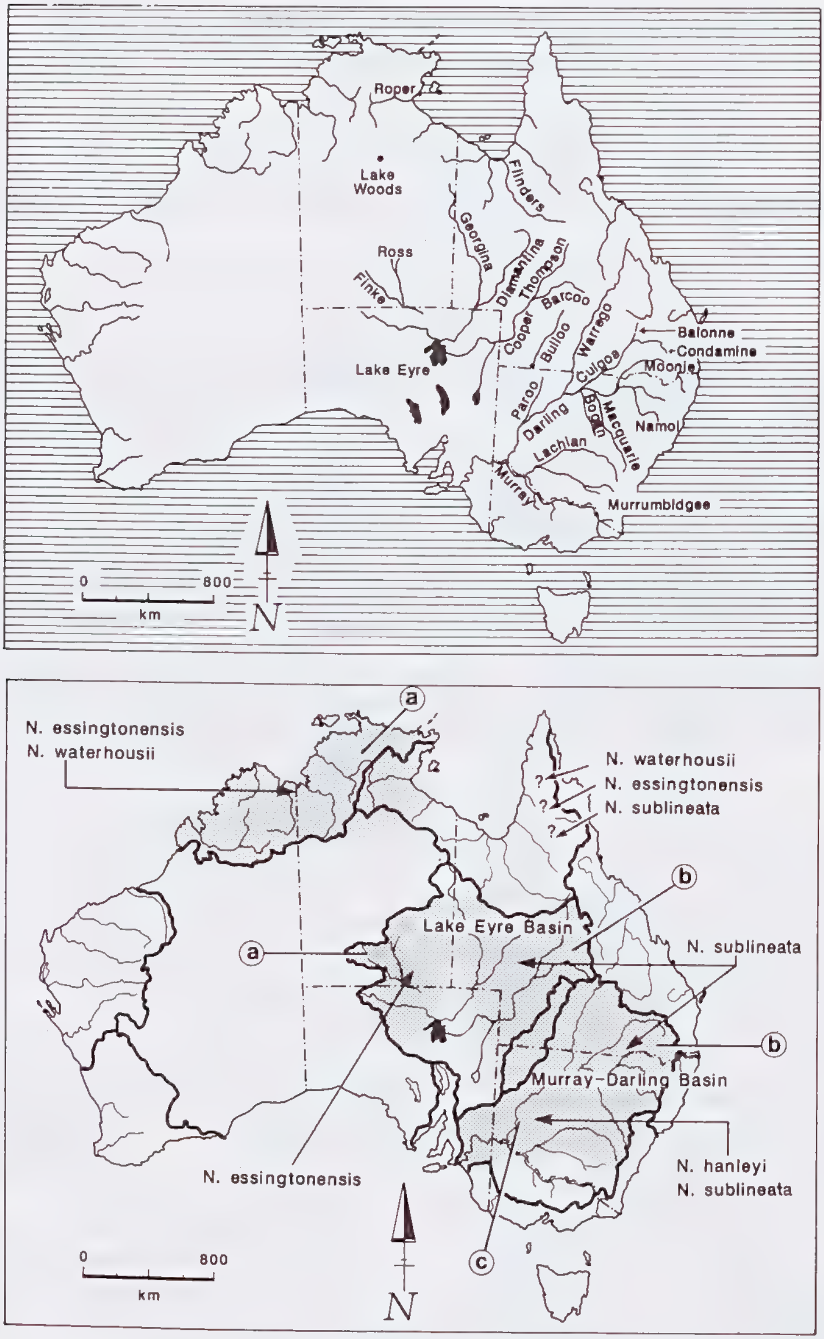

Figure 1. **A.** Rivers from which *Notopala* species used in this study were collected. **B.** Geographical distribution of *Notopala* species in Australia; "a", *N. waterhousii* and *N. essingtonensis*; "b", *N. sublineata*; "c", *N. sublineata* and *N. hanleyi*.

Table 1. Australian species of *Notopala* according to Cotton (1935).

Species	Location
N. hanleyi (Frauenfeld 1864)	River Murray, SA
N. sublineata (Conrad 1850)	Darling River, NSW
N. barretti Cotton 1935	Cooper Creek, SA
N. gatliffi Cotton 1935	Balonne River, Q
N. alisoni (Brazier 1979)	Diamantina River, Q
N. waterhousii (A. Adams and Angas 1864)	North and Central Australia
N. kingi (A. Adams and Angas 1864)	Central and Lower North Australia
N. essingtonensis (Frauenfeld 1862)	Northern Australia
N. tricinta (Smith 1882)	Northern Australia
N. australis (Reeve 1863)	Northern Australia
N. affinis (von Martens 1865)	North-west Australia
N. dimidiata (Smith 1882)	Victoria River, Northern Australia

TAXONOMY

Cotton (1935b) proposed that *Notopala* contained 12 species in Australia (Table 1), five from central and southern regions and seven from the north and north-west. Iredale (1943) suggested that *N. gatliffi* was synonymous with *N. sublineata*, and that both *N. australis* and *N. affinis* were synonymous with *N. essingtonensis*. Stoddart (1982) recognised only two species from northern Australia, namely *N. essingtonensis* and *N. waterhousii*. Current synonymies (Smith, 1992) are shown in Table 2, and broad geographic distributions of taxa are illustrated in Figure 1.

Apart from the early work of Cotton (1935a; 1935b), little is known of central and southern Australian *Notopala*. Smith (1978) listed *Vivipara* (*Notopala*) *hanleyi* from the Murray-Darling Basin, but with no rationale for the generic reassignment. Smith and Kershaw (1979) listed only *Vivipara* (*Notopala*) *sublineata* from the Murray-Darling Basin. Smith (1992) listed both *N. hanleyi* and *N. sublineata* from the Murray-Darling Basin, but gave no indication as to which, if either, occurs in the Lake Eyre Basin. The status of *N. barretti*, described by Cotton (1935b) from the Lake Eyre Basin, is uncertain (Smith, 1992).

Table 2. Synonomies for *Notopala* species according to Smith (1992)

N. hanleyi (Frauenfeld 1864)	*Paludina intermedia* Reeve 1863 *Paludina hanleyi* Frauenfeld 1864 *Paludina (Vivipara) purpurea* von Martens 1865
N. sublineata (Conrad 1850)	*Paludina sublineata* Conrad 1850 *Paludina polita* von Martens 1865 *Notopala gatliffi* Cotton 1935
N. waterhousii (A. Adams and Angas 1864)	*Vivipara waterhousii* A. Adams and Angas 1864 *Vivipara kingi* A. Adams and Angas 1864 *Vivipara alisoni* Brazier 1879
N. essingtonensis (Frauenfeld 1862)	*Vivipara essingtonensis* Frauenfeld 1862 *Paludina ampullaroides* Reeve 1863 *Paludina australis* Reeve 1863 *Paludina affinis* von Martens 1865 *Vivipara dimidiata* Smith 1882 *Vivipara tricinta* Smith 1882
N. barretti Cotton 1935	*Incertae sedis*

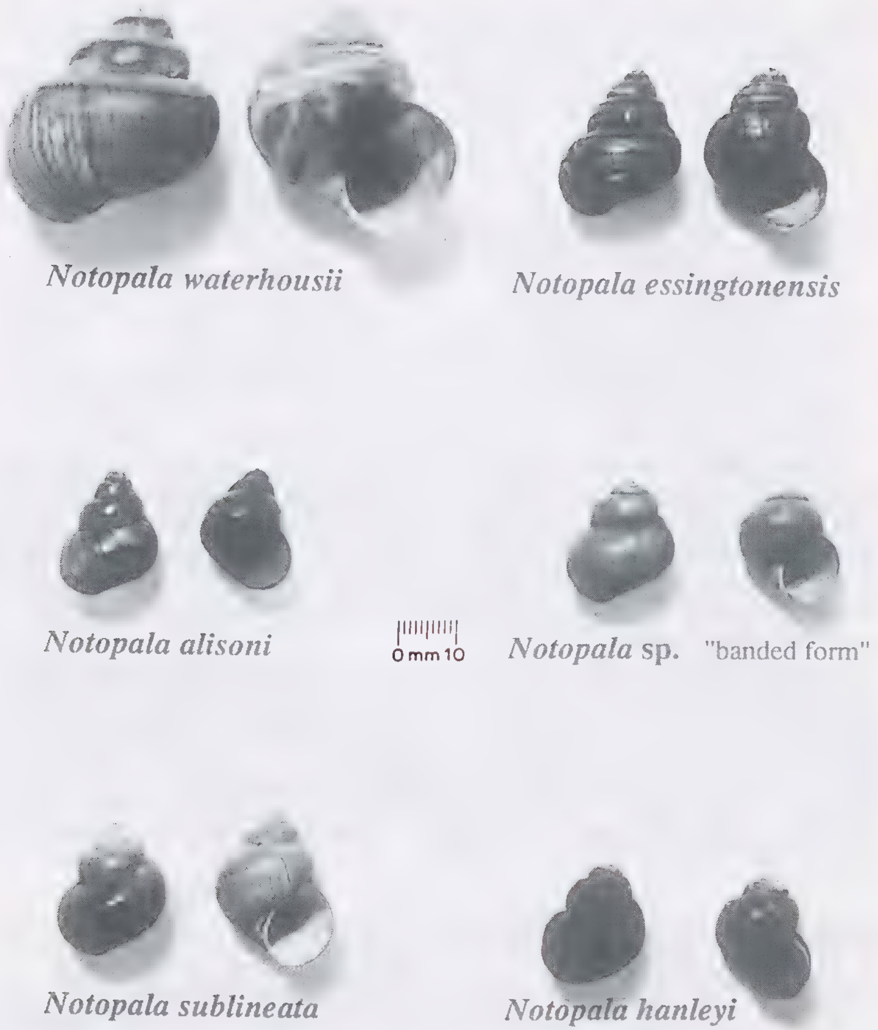

Figure 2. Shell of *N. waterhousii* from the Lake Woods population (C119833). Shell of *N. essingtonensis* from the Fogg Dam population (C76420). Shell of *N. alisoni* from the Alligator Creek, Q, population (C172746). Shell of *Notopala* sp. "banded form" from the Moonie River, NSW, population (C110257). Shell of *N. sublineata* from the Lake Goolangirie population (C172040). Shell of *N. hanleyi* from the Kingston Irrigation Pipeline population (C172039).

Shells of Australian *Notopala* are typical of the family, with convex whorls (sometimes angulate below the periphery) and an aperture length approximately half the shell length (Stoddart, 1982). Historically, taxonomic characters have included shell sculpturing, shell colouration and the presence or absence of distinct colour bands. Colour band development is known to vary within species, however, and spiral shell sculpturing is a distinctive characteristic of the genus (Cotton, 1935a). The existence of similar sculpturing in some south-east Asian genera (cf. Stoddart, 1982) suggests that generic relationships may need revision.

Notopala hanleyi was described (Cotton, 1935b) as having a solid, globose shell with a dark green to brown periostracum, and *N. sublineata* was described as green with coarse spiral sculpturing, with faint narrow colour bands in some specimens (Cotton, 1935b) (Figure 2). In *N. waterhousii* the periostracum varies from greenish brown to pale straw-coloured and colour banding, if present, is faint (Cotton, 1935b); the shell also shows extreme development of the umbilicus (Stoddart, 1982). *Notopala waterhousii* is the largest species in the genus, attaining 5cm in length (Cotton, 1935b) (Figure 2). In *N. essingtonensis* the shell is rarely umbilicate but has a dark-green to yellow-brown periostracum (Stoddart, 1982); the shell is also distinguished by three pronounced dark green spiral bands (Cotton, 1935b; Stoddart, 1982) (Figure 2).

Table 3. Localities of sample populations, collection dates and catalogue references from the Australian Museum, Sydney. The taxa are denoted S, *N. sublineata*; H, *N. hanleyi*; A, *N. alisoni*; E, *N. essingtonensis*; W, *N. waterhousii* ; B, banded shells from the Murray-Darling Basin above Bourke, NSW.

Pop	Locality	Catalogue	Collection	No. Shells	Taxon
1	River Murray, V	C110243	1910	3	S
2	River Murray, SA	C172698	1910	1	S
3	River Murray Swamps, V	C2247		2	H
4	Darling River, NSW	C110228	c. 1910	3	H
5	South Australia		c. 1910	1	S
6	Darling River, Bourke NSW	C98388	1974	6	H
7	Condamine River, Cecil Plains, Q	C110259	1950	5	H
8	Darling River, Wilcannia, NSW	C172697	1952	1	S
9	Darling River, Bourke, NSW	C172699	1910	3	S
10	Macquarie River, Buckingay, NSW	C3462		4	S
11	Murrumbidgee River, NSW	C172700	c. 1910	6	S
12	Bogan River, NSW	C172696	c. 1910	2	S
13	Namoi River, NSW	C101257	1975	1	H
14	River Murray, Renmark, SA	C172695	1963	3	H
15	River Murray, SA	C30878		2	H
16	Boomi Creek, Bogan River, NSW	C2499		3	S
17	Bourke (water pipes) NSW	C110235	1957	4	S
18	Cooper Creek, SA	C110261		6	S
19	Cooper Creek, SA	C6538		3	S
20	Cooper Creek, Innamincka, SA	C110524	1975	6	S
21	Barcoo River, Emmett Downs, Q	C110232	1910	3	A
22	Bulloo River, Narrierra, Q	C11240	1944	6	A
23	Flinders River, Hughenden Q	C110165	1978	4	A
24	Thompson River, Longreach, Q	C48733	1921	4	A
25	Thompson River, Aramac, Q	C56507	1930	3	A
26	Manton River, NT	C110493		5	E
27	Fogg Dam, Humpty Doo, NT	C76408		5	E
28	Roper River, NT	C51072		5	E
29	Ross River, NT	C92127		5	E
30	Lake Woods, Newcastle Waters, NT	C119833		10	W
31	Australia			3	B
32	Moonie River, Q	C110257		5	B
33	Darling River, Bourke, NSW	C110251		4	B
34	Moonie River, Q	C33012		3	B
35	Kingston Irrigation Pipeline, SA	C172039	1992	20	H
36	Lake Goolangirie, SA	C172040	1991	20	S

METHODS

Seven shell characteristics were chosen for measurement (Figure 3): shell length (SHL), shell width (SHW), aperture length (APL), aperture width (APW), spire length (SPL), umbilicus width (UMB) and aperture lip length (ALL). Measurements were made to the nearest 0.05mm using dial calipers.

A total of 170 shells from 36 locations (Table 3) was measured. Twenty specimens were obtained from Lake Goolangirie, on the north-west branch of Cooper Creek, South Australia, in December 1991 and 20 from an irrigation pipeline at Kingston, River Murray, South Australia, in July 1992. An additional 130 specimens were measured from collections held in the Australian Museum, Sydney.

Based on descriptions by Cotton (1935b) and Stoddart (1982) and listings by Smith (1992), shells were assigned to *N. waterhousii*, *N. alisoni*, *N. essingtonensis*, *N. sublineata* or *N. hanleyi*. Although Stoddart (1982) suggested that *N. alisoni* is synonymous with *N. waterhousii*, shells labelled as *N. alisoni* in the Australian Museum were readily distinguished from *N. waterhousii* by a much reduced umbilicus, and therefore were kept separate. Due to the uncertain status of *N. barretti* and its close resemblance to *N. sublineata*, shells from Cooper Creek were assigned to the latter species but kept separate from Murray-Darling Basin populations. In the museum collection were some unlabelled shells from Moonie River in the upper region of the Murray-Darling Basin and one population from Bourke on the Darling River, NSW (AMC References: C110257, C110251, C33012). These shells had distinctive colour bands like *N. essingtonensis*, but were much lighter, being pale-green to straw coloured (Figure 2). They did not fit the descriptions of either *N. sublineata* or *N. hanleyi*, and were included in the analysis as "unknowns".

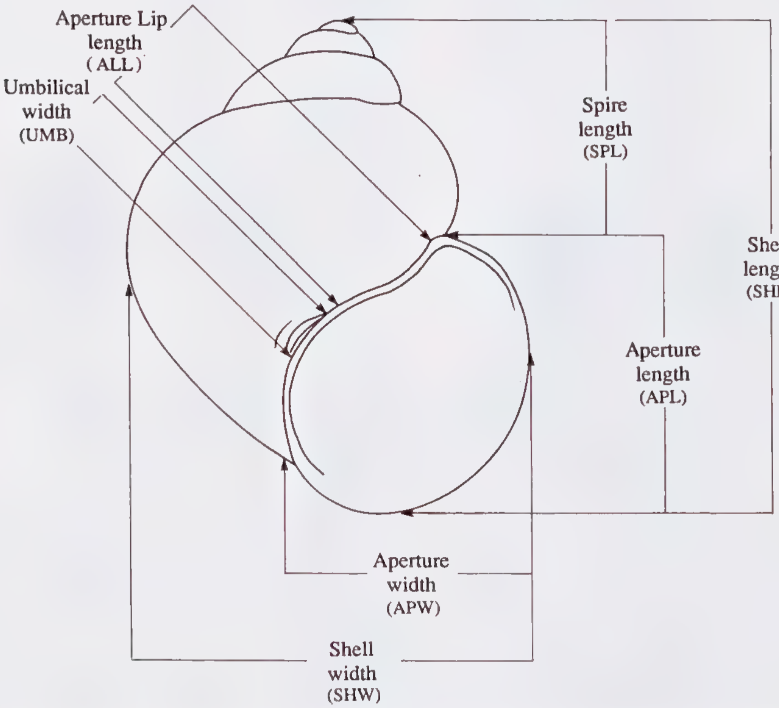

Figure 3. Shell characters.

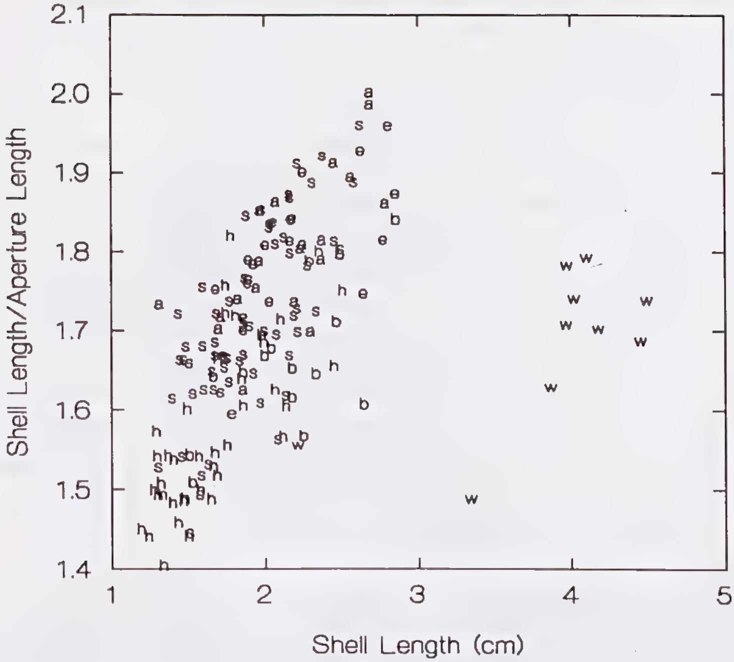

Figure 4. Relationship of shell length to shell length/aperture length for Australian *Notopala*. Species are denoted 's' for *N. sublineata*, 'h' for *N. hanleyi*, 'a' for *N. alisoni*, 'e' for *N. essingtonensis*, 'w' for *N. waterhousii* and 'b' for the banded shells from the upper Murray-Darling Basin.

All statistical computations employed the statistical package SYSTAT v5.0 (Wilkinson, 1990).

RESULTS AND DISCUSSION

Shell Variation in Australian *Notopala*

Stoddart (1982) showed that the ratio of shell length/aperture length to shell length increased less with increasing shell length in *N. essingtonensis* than in *N. waterhousii*. For data from this study (Figure 4), the ratio increases less with increasing shell length in *N. waterhousii* than in all other *Notopala*, including *N. essingtonensis*. This is contrary to Stoddart's (1982) finding, and may indicate significant morphometric differences among populations of *N. waterhousii*. Specimens of *N. waterhousii* measured by Stoddart (1982) had shell lengths of less than 3cm, whereas in this study specimens were distinctly different from all other *Notopala* examined, being larger and having a well-developed umbilicus (Table 4.). The relationship of shell length/aperture length to shell length may therefore not be linear for *N. waterhousii*.

Visual examination of the different *Notopala* suggests that neither shell length nor aperture length are key characters in differentiating species. Principal Components Analysis (PCA) was employed (using Pearson correlation coefficient with VARIMAX rotation) to isolate the characters that account for most variation between species. Shells were ordinated using all seven measurements.

Table 4. Measured shell characters for each *Notopala* species. See Figure 3 for explanation of characters.

Characters Species	n		SHL	APL	SHW	UMB	APW	SPL	ALL
N. alisoni	20	$\bar{x}$	2.159	1.191	1.63	0.259	0.977	1.478	0.535
		±*SE*	*0.086*	*0.039*	*0.054*	*0.014*	*0.034*	*0.064*	*0.015*
N. essingtonensis	20	$\bar{x}$	2.17	1.2	1.658	0.196	1.01	1.447	0.611
		±*SE*	*0.082*	*0.038*	*0.067*	*0.016*	*0.038*	*0.067*	*0.025*
N. waterhousii	10	$\bar{x}$	3.859	2.284	3.314	0.463	1.888	2.501	1.002
		±*SE*	*0.209*	*0.105*	*0.164*	*0.024*	*0.087*	*0.131*	*0.043*
N. hanleyi	42	$\bar{x}$	1.667	1.05	1.383	0.129	0.852	1.1	0.557
		±*SE*	*0.052*	*0.026*	*0.036*	*0.01*	*0.025*	*0.037*	*0.013*
N. sublineata (Darling)	28	$\bar{x}$	1.832	1.084	1.453	0.205	0.921	1.204	0.524
		±*SE*	*0.063*	*0.024*	*0.04*	*0.012*	*0.026*	*0.039*	*0.016*
N. sublineata (Cooper)	35	$\bar{x}$	1.946	1.106	1.552	0.221	0.889	1.259	0.493
		±*SE*	*0.058*	*0.027*	*0.039*	*0.01*	*0.018*	*0.04*	*0.009*
"Banded" Shells	15	$\bar{x}$	2.215	1.318	1.81	0.206	1.069	1.46	0.642
		±*SE*	*0.110*	*0.053*	*0.08*	*0.011*	*0.045*	*0.079*	*0.029*

In the PCA of all *Notopala* species most variance (91%) was explained by PCI, and PCII accounted for only a minor portion (6%). The first component was correlated with aperture lip length (rotated loading of 0.92), and the second was correlated with umbilical width (rotated loading of 0.91). These two components clearly separated *N. waterhousii* from the other species (Figure 5). Specimens of *N. alisoni* (syn. *N. waterhousii*, according to Stoddart, 1982) and *N. essingtonensis* did not form distinctive clusters.

In most morphometric studies PCI is associated with the overall size of the organism. In this case, however, characters relating directly to shell size (SHL, SHW, APL, APW) had much lower loadings (<0.7) on PCI than did aperture lip length. As the measured specimens of *N. waterhousii* were larger than the other taxa (Table 4), and as this group formed a separate cluster along PCI, shells of this taxon were removed and the data re-examined. Removal of *N. waterhousii* had minimal impact on component loadings of all characters. The first component still correlated with aperture lip length (rotated loading of 0.938), while the second retained its positive loading from umbilical width (rotated loading of 0.934).

Model I one-way ANOVAs were used to compare the a *priori* taxonomic groups based on ALL and UMB. Differences were located using Tukey's Honestly Significant Difference procedure.

Significant differences exist between the taxa in umbilical width ($F_{5,164} = 58.85$; $p<0.001$) and aperture lip length ($F_{5,164} = 50.54$; $p<0.001$). *Notopala waterhousii* has a larger umbilicus and aperture lip than other *Notopala*, including *N. essingtonensis*. *Notopala alisoni*, which differs in both characters from *N. waterhousii*, does not differ in either character from the *N. sublineata* populations of the Lake Eyre Basin. The other northern taxon, *N. essingtonensis*, differs from both *N. hanleyi* and *N. sublineata* in having a larger umbilicus than *N. hanleyi*, and a larger aperture lip than either population of *N. sublineata*. No differences exist in either character between *N. essingtonensis* and banded shells from the upper Murray-Darling Basin.

The "banded" group from the Murray-Darling Basin has a larger umbilicus and aperture

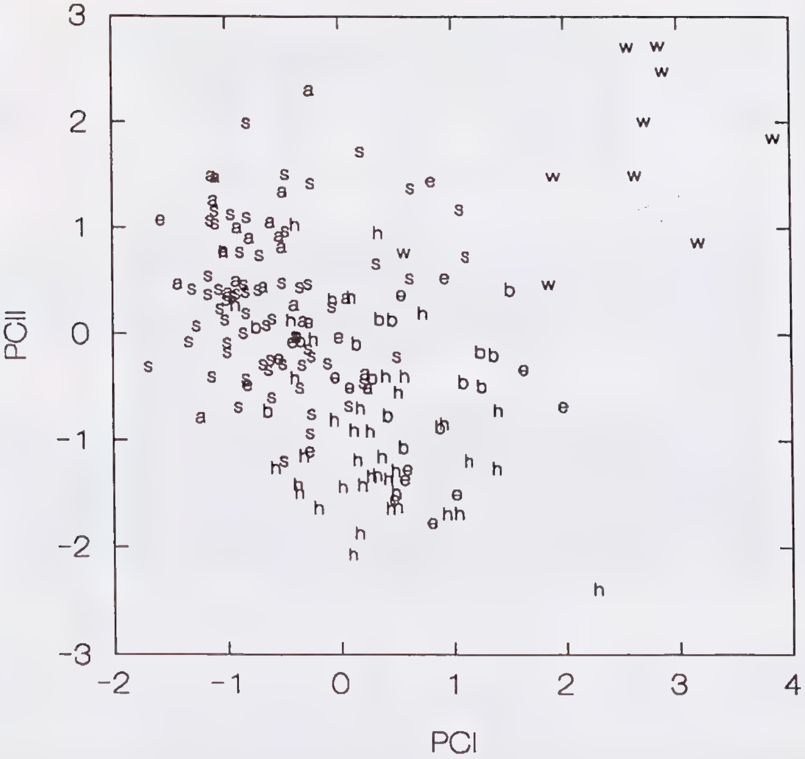

Figure 5. PCA plot for Australian *Notopala*. Species are denoted 's' for *N. sublineata*, 'h' for *N. hanleyi*, 'a' for *N. alisoni*, 'e' for *N. essingtonensis*, 'w' for *N. waterhousii* and 'b' for the banded shells from the upper Murray-Darling Basin.

lip length than *N. hanleyi*, and a larger aperture lip than either population of *N. sublineata*. The umbilicus in *N. hanleyi* is smaller than that in either population of *N. sublineata*. There are no differences in umbilicus width or aperture lip length between *N. sublineata* from the Murray-Darling Basin and the Lake Eyre Basin.

These results suggest that there is at least two species of *Notopala* in central and southern Australia: *N. hanleyi* in the Murray-Darling Basin only, and *N. sublineata* in both the Lake Eyre and Murray-Darling Basins. According to these characters, *N. barretti* may be synonymous with *N. sublineata*. The identity of the "banded" shells from the upper reaches of the Murray-Darling remains unclear, in terms of these morphometric characters they do not appear to belong with either *N. sublineata* or *N. hanleyi*.

Notopala from the Lake Eyre and Murray-Darling Basins

The inclusion of species from northern Australia may obscure variation between groups from the Lake Eyre and Murray-Darling basins. When shells of *N. waterhousii*, *N. essingtonensis*, *N. alisoni* and the "banded" group were removed, the remaining data set comprised 105 shells from 22 populations. PCA was then used to ordinate these shells based on the seven measurements.

In this second PCA the first two components together accounted for only 46% of the total variation. The first component (23%) was positively correlated with umbilical width

Table 5. Numbers of shells assigned to the putative species (rows) by the DFA (columns).

		DFA Groupings		
		"N. hanleyi"	*"N. sublineata"*	Total
Species	*N. hanleyi*	33	9	42
	N. sublineata	5	58	63
	Total	38	67	105

(rotated component loading of 0.911), and component two (also 23%) was correlated with aperture lip length (rotated loading of 0.952). No distinctive clusters were evident, but shells were arranged in two broad groups (Figure 6). Although there was some overlap, most *N. hanleyi* were arranged low on PCI and high on PCII, reflecting a smaller umbilicus and larger aperture lip. The majority of *N. sublineata* shells grouped higher on PCI and lower on PCII.

Discriminant Function Analysis (DFA) was used to assess how accurately individual shells had been assigned to either *N. hanleyi* or *N. sublineata* based on the seven shell characters (Table 5). This suggests that 90% (38/42) of those shells classified as *N. hanleyi* and 92% (63/67) of those classified as *N. sublineata* are 'correctly' assigned.

Overall, this suggests that *N. hanleyi* and *N. sublineata* are morphologically distinctive. The geographical distribution of the shells assigned to each species confirms that both are

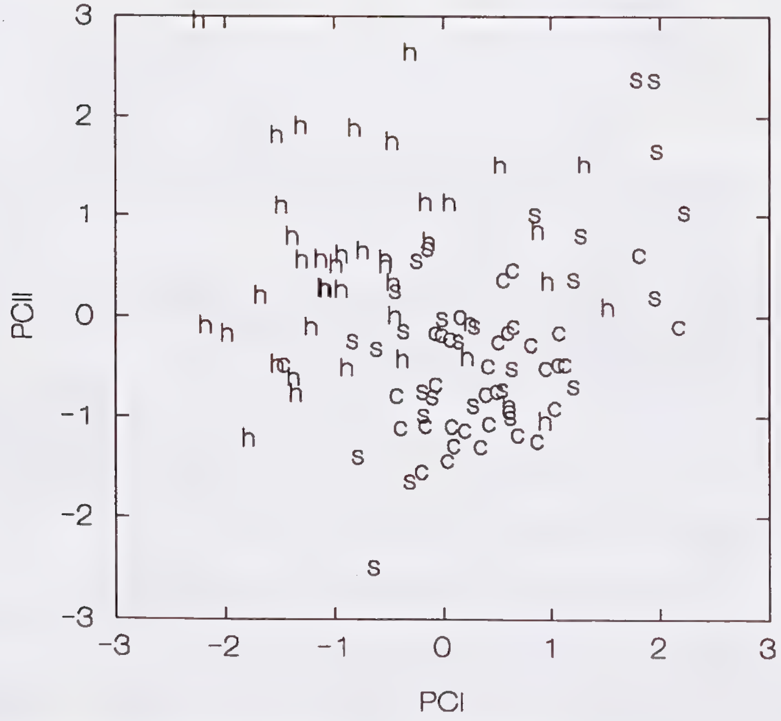

Figure 6. PCA plot for *Notopala* from the Lake Eyre and Murray- Darling basins. Species are denoted 's' for *N. sublineata*, from the Murray-Darling Basin, 'c' for *N. sublineata* from the Lake Eyre Basin and 'h' for *N. hanleyi*.

Table 6. Shell characters (cm) in *N. hanleyi* and *N. sublineata.* The last line shows corresponding values of Student's *t*, with a Bonferroni corrected significance level of p=0.007.

		UMB	SHL	APL	SHW	APW	SPL	ALL
N. hanleyi	$\bar{x}$	0.129	1.667	1.05	1.383	0.852	1.1	0.557
	±SE	*0.01*	*0.052*	*0.026*	*0.036*	*0.025*	*0.037*	*0.013*
N. sublineata	$\bar{x}$	0.213	1.895	1.096	1.508	0.903	1.234	0.507
	±SE	*0.007*	*0.043*	*0.028*	*0.028*	*0.015*	*0.028*	*0.009*
		$p<0.001$	$p<0.001$	$p>0.05$	$p<0.007$	$p>0.05$	$p<0.005$	$p<0.001$

present in the Murray-Darling Basin but that only *N. sublineata* is present in the Lake Eyre Basin.

Aspects of Shell Variation in *N. hanleyi* and *N. sublineata*

Student's *t*-tests were used to examine differences in all measured shell characters between *N. hanleyi* and *N. sublineata* (Table 6). As the shell characters were not independent, the overall error rate was adjusted by the Bonferroni procedure (Neter *et al.*, 1985), where the nominated significance level (0.05) is divided by the number of nonindependent tests. After adjustment, significant differences were evident in umbilicus width, shell length, shell width, spire length and aperture lip length between the two species, with no difference in the shape of the aperture.

Regressions between X (SHL) and Y (SHW, SPL, APL, APW, UMB, ALL) were calculated for each species, and an analysis of covariance (ANCOVA) was applied to test for differences between slopes and elevations (cf. Balaparameswara Rao & Subba Rao, 1985). Again, the error rate was adjusted by the Bonferroni procedure.

Table 7 shows that the relationships of shell length with shell width, spire length, umbilical width and aperture lip length did not differ between the two species. There were

Table 7. Linear regression parameters from the regression of SHW, SPL, APL, APW, UMB, ALL on SHL for *N. hanleyi* (H) (n=42) and *N. sublineata* (S) (n=63). The F ratio (ANCOVA) is used to test the null hypothesis that there is no difference in the slopes of the regressions for the two species (F_s) or no difference in the elevations of the regressions (F_e). A Bonferroni corrected significance level of p=0.007 applies.

	Species	a	b	r^2	df	F
SHL/SHW	H	0.263	0.672	0.963	40	$F_s=2.628$, $p>0.05$
	S	0.391	0.589	0.788	61	$F_e=<1$, $p>0.05$
SHL/SPL	H	-0.04	0.685	0.964	40	$F_s=4.079$, $p>0.01$
	S	0.116	0.589	0.816	61	$F_e=<1$, $p>0.05$
SHL/APL	H	0.261	0.473	0.92	40	$F_s=7.462$, $p<0.007$
	S	0.4	0.367	0.739	61	
SHL/APW	H	0.11	0.445	0.887	40	$F_s=16.24$, $p<0.001$
	S	0.377	0.277	0.591	61	
SHL/UMB	H	-0.06	0.112	0.371	40	$F_s=1.174$, $p>0.05$
	S	-0.05	0.139	0.641	61	$F_e=<1$, $p>0.05$
SHL/ALL	H	0.23	0.195	0.638	40	$F_s=5.281$, $p>0.01$
	S	0.275	0.122	0.357	61	$F_e=<1$, $p>0.05$

differences, however, in the relationships of shell length with aperture length and aperture width.

Notopala hanleyi is morphometrically distinct from *N. sublineata*, at least for the samples on hand. Each has a similar-sized aperture (cf. Table 6), but differs in the relationship of total shell length with both aperture length and aperture width. The smaller aperture, in relation to shell height of *N. sublineata* may increase its ability to avoid desiccation. Stoddart (1982) found that *N. waterhousii* had a smaller aperture in relation to total shell length than *N. essingtonensis*. *Notopala waterhousii* inhabits temporary water-bodies, apparently avoiding desiccation when water-bodies dry by sealing the aperture and resting in the mud whereas *N. essingtonensis* is restricted to permanent water (Stoddart, 1982). Laboratory observations suggest that *N. sublineata* is able to avoid dehydration by tightly sealing the aperture with the operculum, surviving at least three weeks out of water (Sheldon, unpublished).

CONCLUSIONS

Shells of Australian *Notopala* are morphometrically similar, with most variation between species occurring in the size of the umbilicus. The umbilicus is an important taxonomic character in many gastropods (Smith & Kershaw, 1979), and although it has not previously been used for differentiating species of *Notopala*, it may prove useful in future revisions. The size of the umbilicus may have significance for the ecology of species, as a larger umbilicus may be the result of a reduction in the size of the aperture. The umbilicate species *N. waterhousii* and *N. sublineata* have smaller apertures in relation to shell length than other *Notopala*, and avoid dehydration by tightly sealing the aperture with the operculum (Stoddart, 1982).

Taken with the results of Stoddart (1982), these data suggest (but do not confirm) that there are four species of *Notopala* in Australia: *N. waterhousii* and *N. essingtonensis* in drainages across the north and north-west of the continent, *N. sublineata* in the central Lake Eyre and southern Murray-Darling Basins, and *N. hanleyi* in the Murray-Darling system. The status of the "banded" shells from the upper reaches of the Murray-Darling remains unresolved but they may be morphometrically distinctive, judging from the characters used in this analysis. Further studies, utilising additional morphological and molecular characters, are required before their taxonomic status can be formally determined.

Over the past 40 years gastropod populations in the rivers of the Murray-Darling Basin have declined markedly, probably because of environmental changes associated with river regulation (cf. Walker *et al.*, 1992; Sheldon & Walker, 1993). In the lower River Murray both *N. hanleyi* and *N. sublineata* are apparently extinct in the natural environment. *Notopala hanleyi* survives, however, in at least one irrigation pipeline in the South Australian Riverland (Sheldon & Walker, 1993), where it is regarded as a troublesome pest. This places the species in a situation that is both paradoxical and precarious.

Notopala sublineata appears to be extinct in the Murray-Darling Basin, as no live specimens have been recorded in at least 10 years (Sheldon & Walker, 1993). However, it is still abundant in Cooper Creek in the Lake Eyre Basin (Sheldon, unpublished). This population is the only known surviving population of *N. sublineata*.

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